FIRST RECORD OF HARLANJOHNSONELLA ANNULATA ELLIOTT IN GRANIER & DELOFFRE, 1993, NON 1968, A TRIPLOPORELLACEAN ALGA IN UPPER BARREMIAN-LOWERMOST BEDOULIAN STRATA OF LEBANON

Sibelle Maksoud, Bruno Granier, Dany Azar

FIRST RECORD OF *HARLANJOHNSONELLA ANNULATA* ELLIOTT IN GRANIER & DELOFFRE, 1993, NON 1968, A TRIPLOPORELLACEAN ALGA IN UPPER BARREMIAN-LOWERMOST BEDOULIAN STRATA OF LEBANON

Sibelle Maksoud[1], Bruno Granier[2] & Dany Azar[3]

Received: 04 April 2014 / Accepted: 13 September 2014 / Published online: 13 October 2014

Abstract *Harlanjohnsonella annulata* Elliott in Granier & Deloffre, 1993, non 1968, was originally described from Cenomanian strata in Serbia. Herein, we report its first occurrence outside the type area, *i.e.*, in Lebanon, and in older strata, *i.e.,* earliest Bedoulian or Late Barremian in age. Our specimens are compared with topotypic material. The species was recently revised by Radoičić & Schlagintweit who transferred it to the genus *Dissocladella*. However, we never observed any secondary branch and therefore we cannot agree with their interpretation. In addition on the basis of calculations and comparisons of the volume ratio of several species, either fossil (*Montiella elitzae* and *Triploporella steinmannii)* and living (*Dasycladus vermicularis* and *Neomeris dumetosa*) Dasycladalean algae, we assume that *Harlanjohnsonella annulata* was more probably an endosporate form rather than a cladosporate form.

Keywords: Anti-Lebanon, Cretaceous, Barremian, Bedoulian, Jezzinian regional stage, Falaise de Blanche, Dasycladales, *Triploporellacean* alga.

INTRODUCTION

It has been almost half a century since Elliott (1968) described his *Harlanjohnsonella annulata* from Upper Cretaceous ("possibly Cenomanian") strata of Zlatibor (Serbia, former Yugoslavia). There has been no further record since then outside the type region, except for Jaffrezo *et al.* (1980) who mention a "*Harlanjohnsonella* cf. *annulata"* from Aptian strata of Bey Daglari (Turkey). Recently, Radoičić (1995) and Radoičić and Schlagintweit (2010) reexamined some topotypic material, *i.e,* material originating from Cenomanian strata of the type region in western Serbia. In the later publication (Radoičić & Schlagintweit, 2010), they proposed to transfer the species to the genus *Dissocladella,* a proposal that we do not support.
Our paper documents the first occurrence of *Harlanjohnsonella annulata* in older strata, *i.e.*, at the transition of the Barremian to the Bedoulian stage in Lebanon. We describe this Lebanese material, compare it to topotypic material (which consists on nine thin sections of the Collection Deloffre, Leg. Radoičić) and with the Turkish material of the Collection Jaffrezo (to review this determination), and discuss its reproductive strategy together with those of some other Dasycladalean algae.

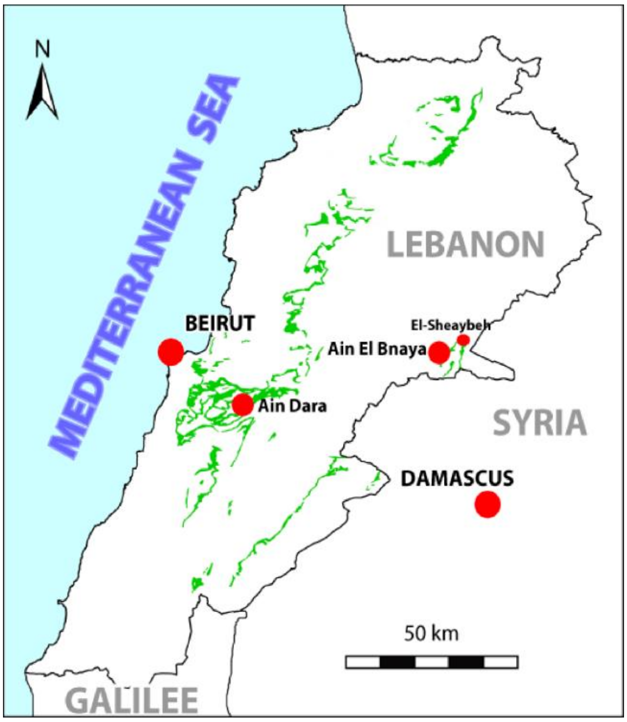

Fig. 1 Location of the outcrops: El-Sheaybeh in Anti-Lebanon and Ain Dara in Mount-Lebanon

GEOLOGICAL SETTING AND MATERIAL

Our material was collected in El-Sheaybeh, a locality NE of Ain el Bnaya, Anti-Lebanon (Fig. 1), Caza Baalbek, Mohafazat Baalbek-Hermel, Eastern Lebanon. There the limestones bearing *Harlanjohnsonella annulata* Elliott in Granier & Deloffre are referred to the Jezzinian Regional Stage (Maksoud *et al*., 2014). The alga is common in these bioclastic wackestones (Fig. 2); its large thalli are visible, even without lens, on polished rock slabs (Fig. 3). It occurs in 40 layers out of 67 in a log section 17 m in height. It is also found East of Ain Dara, Mount-Lebanon (Fig. 1), where it appears in 17 layers out of 71 in a log section 55 m in height. We prepared forty thin sections as well as some acetate peels from selected limestone samples.

[1] Université de Bretagne Occidentale (UBO), UMR 6538 Domaine Océanique, 6, avenue Le Gorgeu - CS 93837, 29238 Brest Cedex 3 (France); sibelle.maksoud@univ-brest.fr
[2] Department of Ecology and Evolutionary Biology, The University of Kansas, 1200 Sunnyside Avenue, Lawrence, Kansas 66045 (USA); bgranier@ku.edu
[3] Lebanese University, Faculty of Science II, Fanar, Natural Sciences Department, Fanar - El-Matn, PO box 26110217 (Lebanon); azar@mnhn.fr

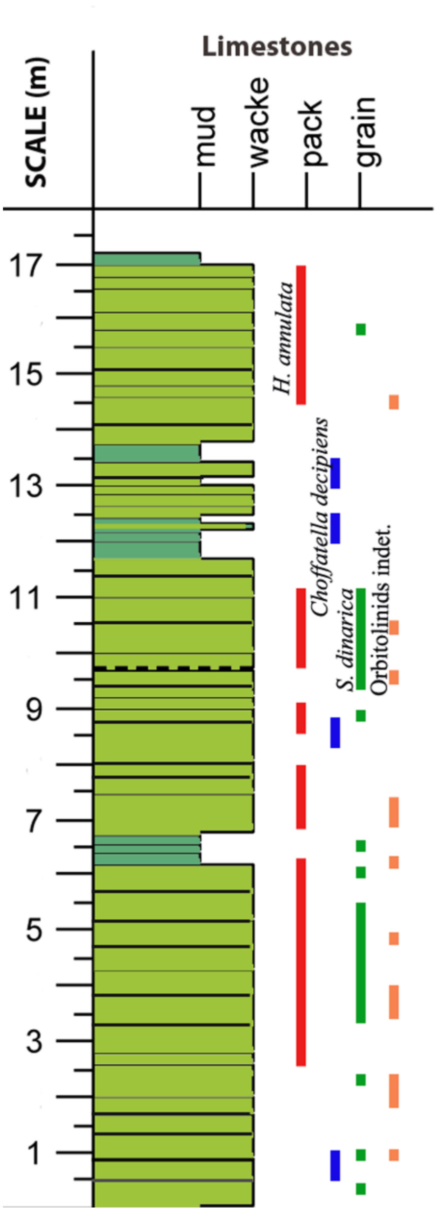

Fig. 2 Stratigraphic section in El-Sheaybeh (coordinates are 33°55'8.83''N; 36°14'8.88''E) with distribution of *Harlanjohnsonella annulata* Elliott in Granier & Deloffre in red, *Choffatella decipiens* (Schlumberger) in blue, *Salpingoporella* (*Hensonella*) *dinarica* Radoičić in green, and indeterminate orbitolinids in orange.

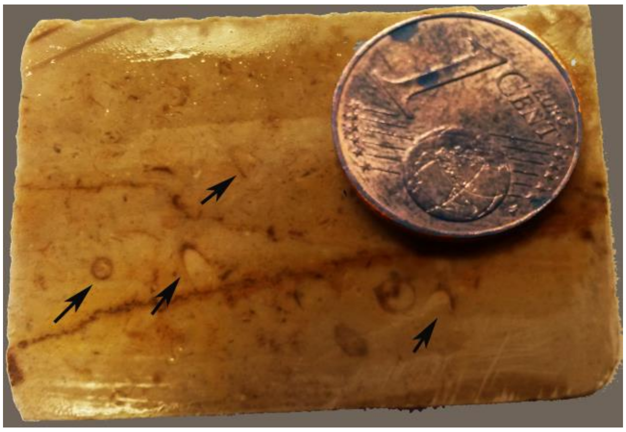

Fig. 3 Specimens of *Harlanjohnsonella annulata* as seen on polished rock slabs (Sample VO15).

SYSTEMATICS

Phyllum: Chlorophyta
Class: Dasycladophyceae Hoek *et al.*, 1995
Order: Dasycladales Pascher, 1931
Family: Triploporellaceae (Pia, 1920)
Tribe : Salpingoporelleae Bassoullet *et al.*, 1979
Genus : *Harlanjohnsonella* Elliott in Granier & Deloffre, 1993, non 1968
Harlanjohnsonella annulata Elliott in Granier & Deloffre, 1993, non 1968
Fig. 10a-g ; Fig. 11a-d
Synonymy
1968 *Harlanjohnsonella annulata* sp. nov.- Elliott, p. 494-495, Pl. 93, figs. 1-2 (syntypes); Pl. 94, figs. 1-2 (syntypes); Zlatibor, Serbia, former Yugoslavia, Upper Cretaceous (possibly Cenomanian) (*nomen nudum*).
1978 *Harlanjohnsonella annulata*.- Bassoullet *et al.*, p. 120-121, Pl. 12, figs. 8 (= Elliott, 1968, previously unpublished) - 9 (= Elliott, 1968, Pl. 94, fig. 1) (*nomen nudum*).
v. non 1980 *Harlanjohnsonella* cf. *annulata*.- Jaffrezo *et al.*, Pl. II, fig. 9, Bey Daglari, Ýmeciksusuz section, Sample 881 E10, (?Upper) Aptian (*nomen nudum*)
1993 *Harlanjohnsonella annulata*.- Elliott (in Granier & Deloffre), definition of the lectotype by G.F. Elliott: Pl. "93" (actually numbered 94), fig. 1 of Elliott (1968), nr. 53441 B.M.(N.H.).
1995 *Harlanjohnsonella annulata*.- Radoičić , Pl. 1, fig. 1, Southern Zlatibor, Tetrebovo, Serbia, thin section RR-2943, Lower Cenomanian.
2010 *Dissocladella annulata* nov. comb.- Radoičić & Schlagintweit, p. 55-57, Pl. 1, figs. 1-4; Pl. 2, figs. 1-7; Pl. 3, figs. 1-7; Pl. 4, figs. 1-9; Pl. 5, figs. 1-10 ; Pl. 6, figs. 1-16, W Serbia, Cenomanian.

Original diagnosis:
The diagnosis of the genus and species given by Elliott (1968, p. 494) is as follows: "Weakly calcified thin-walled tubular and annular dasyclad, with successive verticils showing numerous swollen primaries the presumed secondaries not being calcified".

Description:
The different sections suggest an elongated, roughly cylindrical or possibly club-shaped, thallus with a broad axial cavity. The laterals are arranged in verticils, *i.e*, having an euspondyle arrangement, and are more or less set apart. Tangential sections show that the interverticillar space is commonly equal to the height of a verticil (Fig. 10 c), the distance between two verticil planes being commonly twice the height of a verticil. The laterals consist of short, phloiophorous and distally open primaries. We did not observed any secondaries, as reported by Radoičić & Schlagintweit (2010), nor any reproductive structures (cysts).

Remark:
Radoičić and Schlagintweit (2010: Pl. 6, fig. 13) illustrated one specimen with features that they quite convincingly interpreted as secondary ramifications. They also illustrated several oblique sections of fragments displaying tangential cuts (Radoičić &

Schlagintweit, 2010: Pl. 3, fig 7; Pl. 5, fig. 1-6) with features that they also interpreted as secondary ramifications. However, these features are less convincing: they may also be artefacts resulting from the distal arrangement of the laterals, from microborings and micritization, or these fragments may not expressedly refer to the same species. Consequently, in the meantime, we are awaiting new evidences to support their proposal to transfer the species *Harlanjohnsonella annulata* to the genus *Dissocladella* (Pia in L.R. Rao & Pia, 1936) and to treat the genus *Harlanjohnsonella* as a junior synonym of *Dissocladella*.

COMPARAISON OF THE LEBANESE MATERIAL WITH OTHER OCCURRENCES

As stated above, *Harlanjhonsonella annulata* is only known from its type locality: Zlatibor, Serbia, former Yugoslavia (Elliott, 1968; Radoičić, 1995; Radoičić & Schlagintweit, 2010) and eventually from the Ýmeciksusuz section, Bey Dağlari, SW Turkey (Jaffrezo *et al.,* 1980). In the following section, we compare our Lebanese specimens with those from Serbia and Turkey.

Comparison based on the bibliographic data (Tables 1, 3-4)**:**

The average dimensions of our specimens (Table 1) fit quite well with Elliott's (Table 3):

- external diameter D = 2 mm, up to 2.25 mm (Elliott, 1968) ≈ 1.828 ± 0.256 mm (our material);
- distance between successive whorls h = 0.19-0.25 mm (Elliott, 1968) ≈ 0.168 ± 0.015 mm (our material);
- number of laterals per whorl w = 50 (Elliott, 1968) ≈ 42 ± 9 (our material).

The values given by Radoičić and Schlagintweit (2010, here Table 4) show more variability than ours (Table 1). The maximum values of the external diameter "D", the central stem diameter "d" and the distance between successive whorls h are higher than our maximum values.

However, both maximum and minimum values of the diameter of primary pores p of Radoičić and Schlagintweit (2010) fit with the maximum and minimum of our "p": 0,098 - 0,123 mm (Radoičić & Schlagintweit, 2010) ≈ 0,098 - 0,127 mm (our material).

Also, the maximum value of the length of the laterals l matches with our maximum "l": l_{max} = 0,247 mm (Radoičić & Schlagintweit, 2010) ≈ 0,244 mm (our material). The minimum number of laterals per whorl w of Radoičić and Schlagintweit (2010) matches with our minimum "w": w_{min} = 35 (Radoičić & Schlagintweit, 2010) ≈ 36 (our material).

Comparison with the topotypic material (Tables 2-4; Fig. 11a- d)**:**

We measured the specimens from nine thin sections of topotypic material (Collection Deloffre, Leg. Radoičić) and compared them with our material. Both sets of data are quite similar:

- the external diameter D = 1.380 ± 0.211 mm (topotypic material) ≈ 1.828 ± 0256 mm (our material),
- the central stem diameter d = 1.105 ± 0.177 mm (topotypic material) ≈ 1.512 ± 0.256 mm (our material),
- the thickness of the calcareous wall e = 0.137 ± 0.37 mm (topotypic material) ≈ 0.158 ± 0.067 mm (our material),
- the diameter of primary pores p = 0.104 ± 0.018 mm (topotypic material) ≈ 0.117 ± 0.009 mm (our material),
- the distance between successive whorls h = 0.199 ± 0.031 mm (topotypic material) ≈ 0.28 mm (our material),
- the length of the laterals l = 0.126 ± 0.017 mm (topotypic material) ≈ 0.177 ± 0.049 mm (our material).

The major difference is with respect of the number of laterals per whorl w = 31 ± 7 (topotypic material) and less than 42 ± 9 (our material).

Comparison with the Turkish material:

Jaffrezo *et al.* (1980) mentioned an "*Harlanjohnsonella* cf. *annulata"* from Aptian strata of Bey Daglari (Turkey). However, as these authors used "cf." between the generic name and the specific epithet, they did not expressedly ascribed it to the species.

Actually, after checking the thin section, we can confirm it is not referable to *H. annulata*. The illustrated specimen (Jaffrezo *et al.*, 1980: Pl. II, fig. 9; herein Fig. 4) looks more like a *Salpingoporella* sp. with a typical euspondyl arrangement. Due to the quadrangular aspect of its laterals, it can be compared either to *Salpingoporella genevensis* Conrad *et al.,* 1973, or to *S. popgrigorei* Bucur, 2007. The three species have similar h values: 0.088 mm for *Salpingoporella popgrigorei* (Bucur, 2007), 0.09 mm for *S. genevensis* (Conrad *et al.*, 1973), and 0.088 mm for "*Harlanjohnsonella* cf. *annulata"* (Jaffrezo *et al.*, 1980). However other measurements (Table 5) make them easy to distinguish.

ARRANGEMENT OF THE REPRODUCTIVE STRUCTURES

Although Pia (1912, 1920: p. 192 -Austrian edition- p. 191 -French edition-, Granier & Sander, 2013; Granier *et al*. 2013) suggested that the diameter (and consequently volume) of the algal main axis and the final location of the cysts before their release as the alga matures might be correlative, he never addressed this point in detail.

Hereafter we test a new approach and compare the volume ratios of the fertile parts or the parts considered as fertile in fossil (Cretaceous) and living algae, *i.e.*, either the main axis (endosporate), modified primaries (cladosporate) or fertile ampulae (choristosporate). In addition to *Harlanjohnsonella annulata* (our data), we include two fossil Dasycladales algae: *Triploporella steinmanni* Barattolo, 1983 (data from Barattolo, 1983), which is cladosporate, and *Montiella elitzae* (Bakalova, 1971) (our data), which is choristosporate, as well as for two living forms: *Dasycladus vermicularis* (Scopoli, 1772) (data from Berger, 2006) and *Neomeris dumetosa* Lamouroux, 1816 (data from Berger, 2006), both choristosporate.

Fig. 4 "*Harlanjohnsonella* cf. *annulata"*, probably a *Salpingoporella* sp. Collection Jaffrezo, thin section 881 E10 (Scale bar = 0.25 mm).

We first draw schematic reconstruction of each alga to better understand their tridimensional organisation and the distribution of the volumes. In *Harlanjohnsonella* (Fig. 5), a lateral is composed of a cone and half a sphere. For the fossil algae, it consists of a cylinder with an ovale base and three cones for *Triploporella* (Fig. 6) and a cylinder and a spheroid for *Montiella* (Fig. 7). For the living algae, a lateral of *Dasycladus vermicularis* (Fig. 8) requires the combination of a cylinder for the first order, a spheroid for the ampula, four cylinders for the second order, and sixteen cylinders for the third order, while a lateral of *Neomeris dumetosa* (Fig. 9) consists of a cylinder for the first order, a spheroid for the ampula, and two cylinders with each a spheroid for the second order.
Calculations are the made for *Harlanjohnsonella* (using our data: Table 1), for *Triploporella steinmanni* (using data from Barattolo, 1983: Table 6), for *Montiella elitzae*

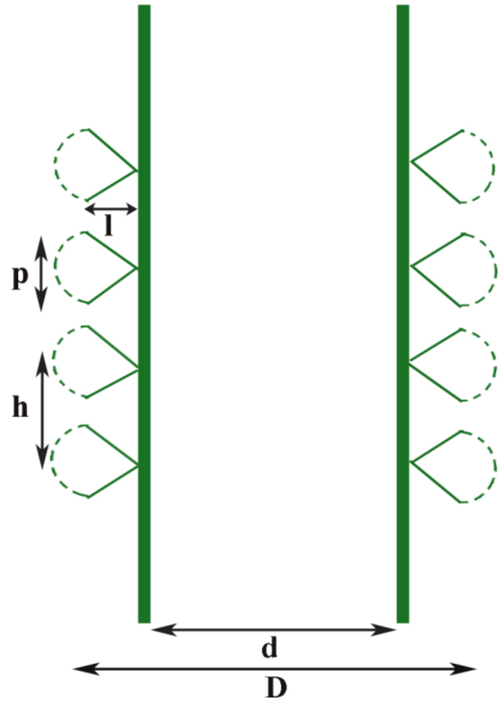

Fig. 5 Schematic reconstruction of *Harlanjohnsonella annulata* Elliott in Granier & Deloffre, 1993.

(using our data: Table 7), for *Dasycladus vermicularis* (using data derived from Berger, 2006: Table 8) and for *Neomeris dumetosa* (using data derived from Berger, 2006: Table 9). For each Cretaceous and modern algae, we calculate the relative ratio (R0) of the axis volume (V0) to the total volume of a verticillar interval, that of the corresponding volume of laterals (Vs + VF), and that (RF) of the corresponding volume of the sole fertile parts (VF). The results are compared and discussed.

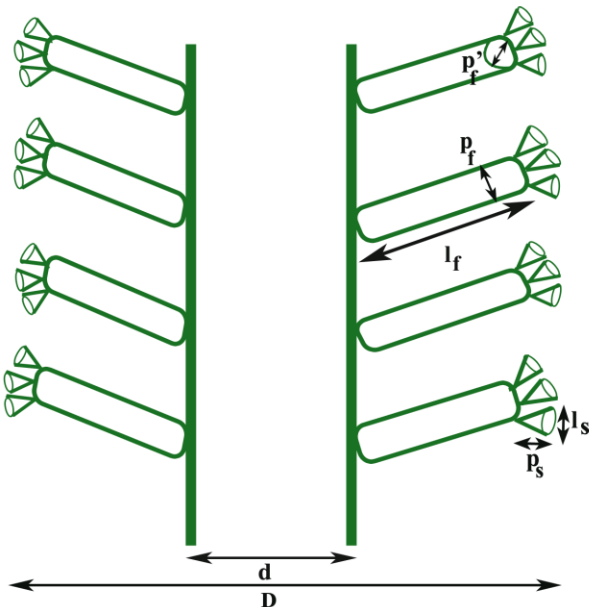

Fig. 6 Schematic reconstruction of *Triploporella steinmannii* Barattolo, 1983.

The verticillar volume of the stem, the fertile laterals and the sterile laterals are presented in the tables below (Tables 8-13).

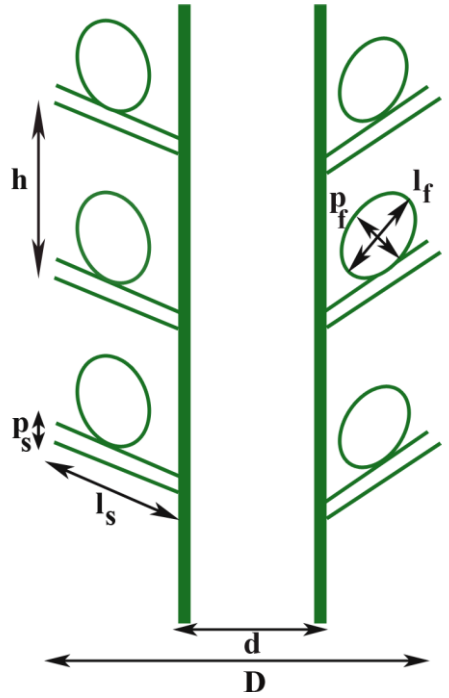

Fig. 7 Schematic reconstruction of *Montiella elitzae* (Bakalova, 1971).

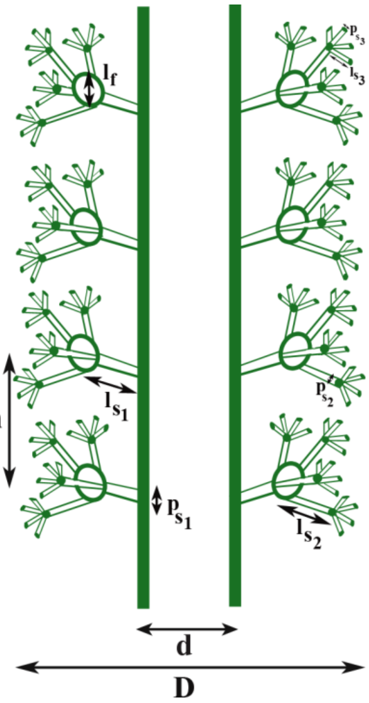

Fig. 8 Schematic reconstruction of *Dasycladus vermicularis* (Scopoli, 1772).

The executed calculations for each alga are the following:

- For *Harlanjohnsonella annulata* (Tables 1, 10):

As a starting hypothesis (1) we consider that the laterals of Harlanjohnsonella are fertile and its main axis sterile (cladosporate).

For each verticil, the volume of the stem is equal to a cylinder volume:

$V0 = \pi*h*d^2/4 = 0.302$ mm^3

The volume of a lateral is equal to the sum of a cone and half a sphere volumes:

$vf = [(\pi*l*p^2 /12)] + [\pi*p^3/12] = [\pi*(p + l)*p^2]/12 = 0.001$ mm^3

The total volume of the laterals is equal to:

$VF = w*vf = 0.045$ mm^3

The resulting rates are:

$R0 = RS = [V0/(VF+V0)]*100 = [0.288 / (0.045 + 0.288)]*100 = 87.06$ % for the stem only (the "sterile" part);

$RF = [VF/(VF+V0)]*100 = [0.045 / (0.045 + 0.288)]*100 = 12.94$ % for the laterals (supposed "fertile" in this starting hypothesis).

In the alternative hypothesis (2) we consider that the laterals of *Harlanjohnsonella* are sterile and its main axis fertile (endosporate).

The resulting rates are:

$R0 = RF = [V0/(VS+V0)]*100 = [0.288 / (0.045 + 0.288)]*100 = 87.06$ % for the stem only (the "fertile" part);

$RS = [VS/(VS+V0)]*100 = [0.045 / (0.045 + 0.288)]*100 = 12.94$ % for the laterals (supposed "sterile" in this alternative hypothesis).

- For *Triploporella steinmannii* (Tables 6, 10) :

The biometric data are from Barattolo (1983). When an average value is not available, we use the maximal value.

For each verticil, the volume of the stem is equal to a cylinder volume:

$V0 = 0.46$ mm^3

The primaries are fertile (with visible reproductive structures). The volume of a primary lateral is equal to a cylinder with elliptic base volume:

$vf = \pi*l*p1*p1'/4 = 0.1381$ mm^3

The volume of a secondary is equal to a cone volume:

$v2 = \pi*l2*p2*p2'/12 = 0.0015$ mm^3

The total volume of the sterile part in a verticil is equal to: $VS = V0 + w*w'*v2 = 0.6019$ mm^3

The total volume of the fertile part in a verticil is equal to the volume of the primary laterals:

$VF = w*vf = 4.2410$ mm^3

The resulting rates are:

$R0 = 9.50$ % for the stem only.

$RS = 12.43$ % for the whole sterile part (including the stem).

$RF = 87.57$ % for the fertile part.

The volume ratio of the fertile part in the laterals is: $R (F/F+S) = 90.87$ %

- For *Montiella elitzae* (Tables 7, 10, Fig. 10h-j):

For each verticil, the volume of the stem is equal to a cylinder volume:

$V0 = 0.005$ mm^3

The volume of a sterile lateral is equal to a cylinder volume:

$vs = \pi*ls*ps^2/4 = 0.001$ mm^3

The total volume of the sterile laterals is:

$Vs = w*vs = 0.006$ mm^3

The total volume of the sterile part is:

$VS = V0 + w*vs = 0.011$ mm^3

The volume of a fertile lateral is equal to a spheroid volume:

$vf = (4/3)*\pi*(lf/2)*(pf/2)^2 = \pi*lf*pf^2/6 = 0.002$ mm^3

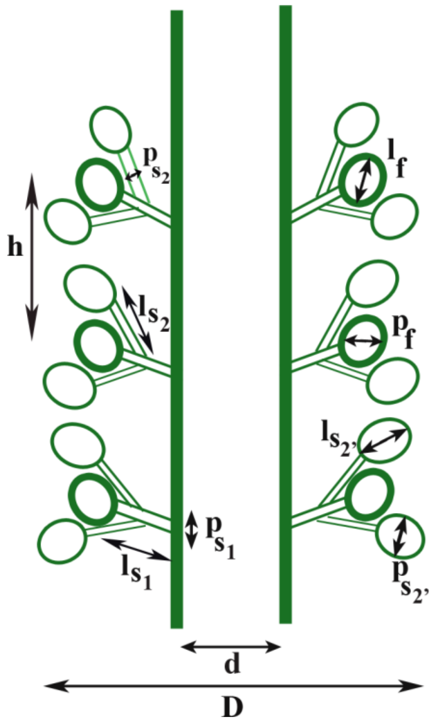

Fig. 9 Schematic reconstruction of *Neomeris dumetosa* Lamouroux, 1816.

The total volume of the fertile part is:
VF= w*vf = 0.019 mm^3
The resulting rates are:
R0 = [V0/(VS+VF)]*100 = [0.005 / (0.011 +0.019)]*100 = 16.81 % for the stem only.
RS = [VS/(VS+VF)]*100 = [0.011 / (0.011 +0.019)]*100 = 36.24 % for the whole sterile part (including the stem)
RF = [VF/(VS+VF)]*100 = [0.019 / (0.011 +0.019)]*100 = 63.76 % for the fertile part.
The volume ratio of the fertile part in the laterals is: R (F/F+S) = vf/(vf+vs) = 76.64 %

- For *Dasycladus vermicularis* (Tables 8, 11) :

For each verticil, the volume of the stem is equal to a cylinder volume:
V0 = 0.0835 mm^3
The volume of a sterile lateral is equal to:
vs = vs1 + 4vs2 + 16vs3 = (π*ls1*ps1^2/4) + 4(π*ls2*ps2^{2}π*/4) + 16(π*ls3*ps3^{2}π*/4) = 0.0150+(4*0.0010) + (16*0.0001) = 0.0209 mm^3
The volume of sterile laterals per verticil is:
Vs = w*vs = 0.2091 mm^3
The sterile volume per verticil is:
VS = V0 + Vs = 0.2926 mm^3
The volume of a fertile lateral is equal to a sphere volume:
vf = pf3π /6 = 0.0141 mm^3
The fertile volume per verticil is:
VF = w vf = 0.1414 mm^3
The resulting rates are:
R0 = [V0/ (VS+VF)]*100 = 19.24 % for the stem only.
RS = [VS/ (VS+VF)]*100 = 67.42 % for the whole sterile part (including the stem).
RF = [VF/ (VS+VF)]*100 = 32.58 % for the fertile part.
The volume ratio of the fertile part in the laterals is: R (F/F+S) = vf/(vf+vs) = 40.34 %

- For *Neomeris dumetosa* (Tables 9, 12):

For each verticil, the volume of the stem is equal to a cylinder volume:
V0 = 0.0046 mm^3
The volume of a sterile lateral is equal to the sum of one cylinder (R1), plus two more cylinders and two spheroids (R2):
vs = vs1 + 2 (vs2 + vs2’) = (π*ls1*ps1^2/4) + (π*ls2*ps2^2 /4) + [π*ls2’*(ps2’)^2/6] = 0.0017 mm^3
The volume of sterile laterals per verticil is:
Vs = w*vs = 0.0465 mm^3
The sterile volume per verticil is:
VS = V0 + Vs = 0.0511 mm^3
The volume of a fertile lateral is equal to a spheroid volume:
vf = (4/3 π) (pf/2)2(lf/2) = π/6 pf2 lf = 0.0005 mm^3
The fertile volume per verticil is:
VF = w*vf = 0.0153 mm^3
The resulting rates are:
R0 = [V0/ (VS+VF)]*100 = 6.90 % for the stem only.
RS = [VS/ (VS+VF)]*100 = 76.88 % for the whole sterile part (including the stem).
RF = [VF/ (VS+VF)]*100 = 23.12 % for the fertile part.
The volume ratio of the fertile part in the laterals is: R (F/F+S) = vf/(vf+vs) = 24.83 %

DISCUSSION (Table 13)

The ratios of the stem and those the laterals to the total volume are the following:

a. *Harlanjohnsonella annulata*: R0 (stem) = 87.1 % >>> R (laterals) = 12.9 %
b. *Triploporella steinmanni*: R0 (stem) = 9.5 % <<< V (laterals) = 90.5 %
c. *Montiella elitzae*: V0 (stem) =16.8 % <<< V (laterals) = 83.2 %
d. *Dasycladus vermicularis*: V0 (stem) = 19.2 % <<< V (laterals) = 80.8 %
e. *Neomeris dumetosa*: V0 (stem) = 6.9 % <<< V (laterals) = 93.1 %

In the studied cladosporate and choristosporate species, the volume of the stem is not representing more than 20% of the cytoplasm. However, it is not the case for *Harlanjohnsonella annulata* with by far the most voluminous stem.

The ratios of the fertile laterals to the total volume are the following:

a. *Harlanjohnsonella annulata*: 12.9 % (hypothesis 1) or 0 % (hypothesis 2)
b. *Triploporella steinmanni*: 87.6 %
c. *Montiella elitzae*: 63.8 %
d. *Dasycladus vermicularis*: 32.6 %
e. *Neomeris dumetosa*: 23.1 %

These ratios decrease significantly from the cladosporate (*Triploporella steinmanni*) to the choristosporate forms (*Montiella elitzae*, *Dasycladus vermicularis*, *Neomeris dumetosa*). Again, *Harlanjohnsonella annulata* is out of the general frame.

If now we consider the ratios of the fertile parts to the total volume, we get similar results except for *Harlanjohnsonella annulata*, which pass to 87.1 % in the case of hypothesis 2. This ratio is close to that of *Triploporella steinmanni* (87.6 %).

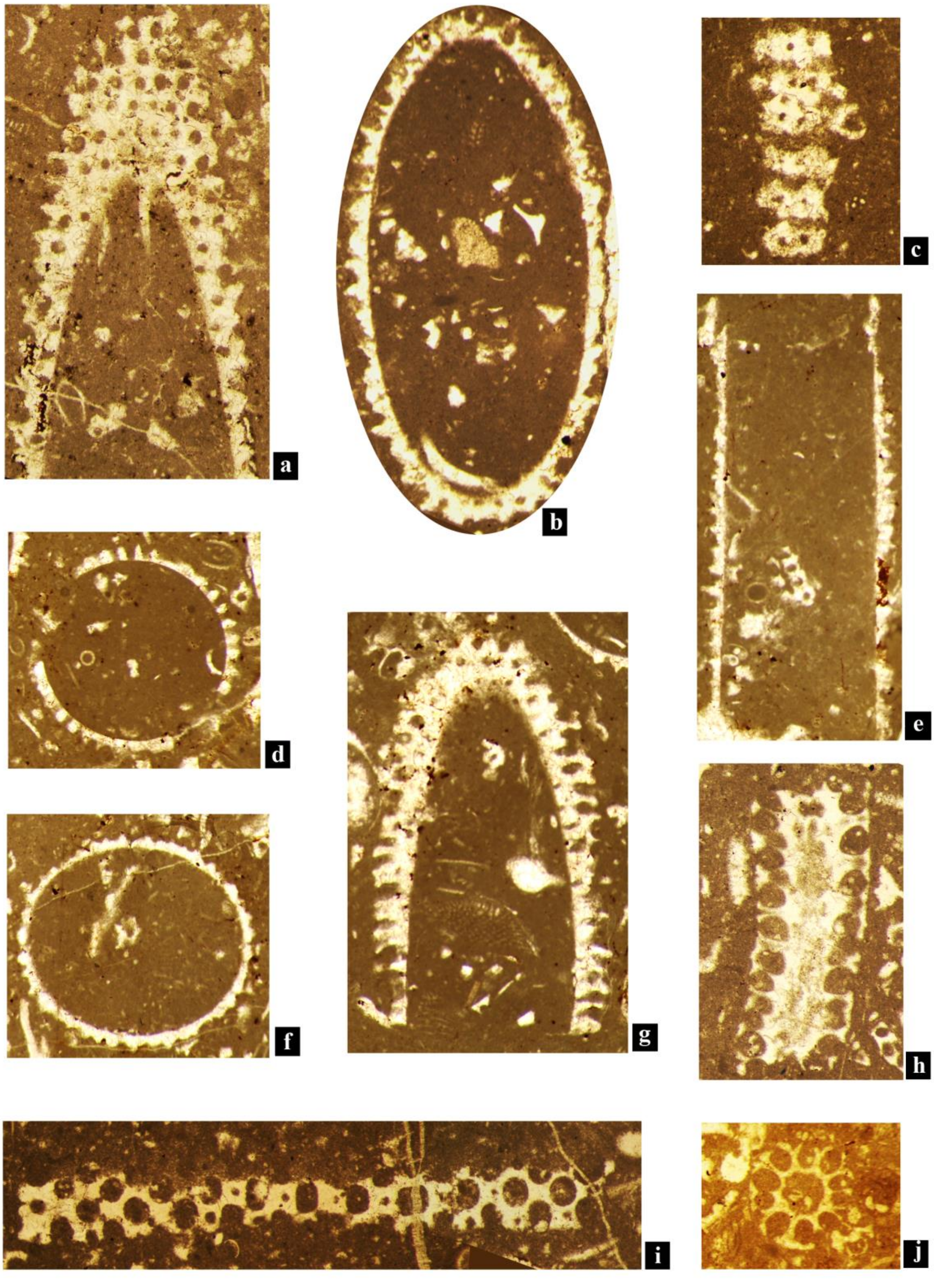

Fig. 10 a-g *Harlanjohnsonella annulata* Elliott in Granier & Deloffre, 1993, non 1968; **a** Oblique section, El-Sheaybeh, Jezzinian, thin-section VO15 ; **b** Oblique section, El-Sheaybeh, Jezzinian, thin-section VO11; **c** Tangential section - El-Sheaybeh, Jezzinian, thin-section VO11; **d** Transverse section - El-Sheaybeh, Jezzinian, thin-section VO 15. **e** Axial section - El-Sheaybeh, Jezzinian, thin-section VO 15; **f** Oblique-Trasverse section - El-Sheaybeh, Jezzinian, thin-section VO 15; **g** Oblique section, El-Sheaybeh, Jezzinian, thin-section VO15. **h-j** *Montiella elitzae* (Bakalova, 1971); **h** Longitudinal section - East Ain Dara, Jezzinian, thin section EAD19; **i** Transverse section - East Ain Dara, Jezzinian, thin-section EAD18; **j** Tangential section - Maarab, Jezzinian, thin-section MEB45. All scale bars = 0.5 mm, (black bar: a-c and h-j; blue bar: d-g)

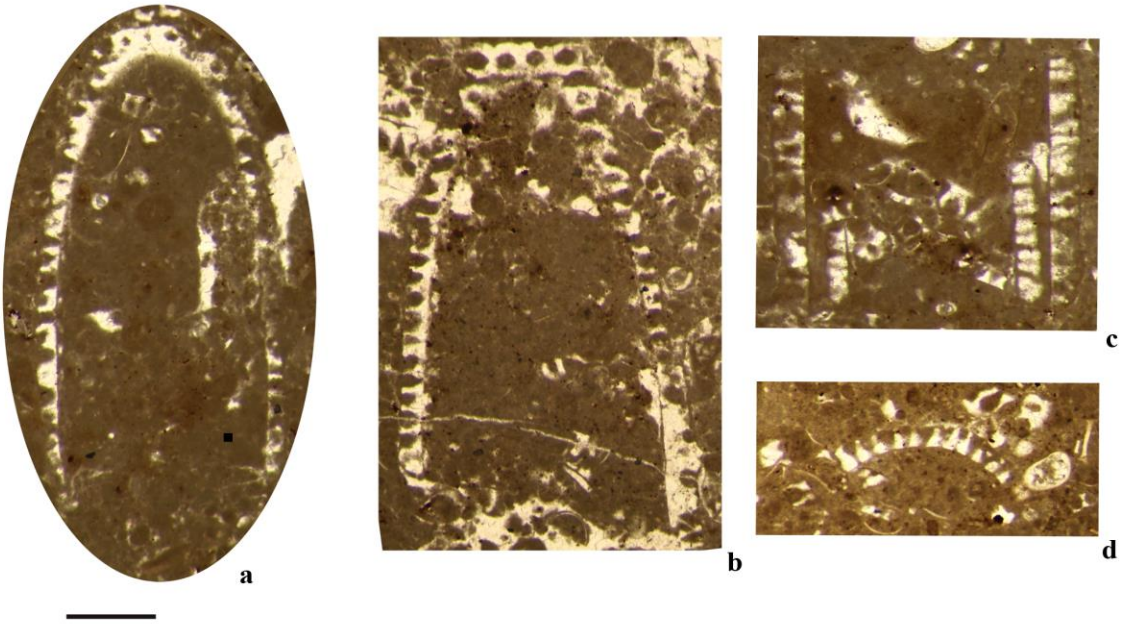

Fig. 11 a-d *Harlanjohnsonella annulata* Elliott in Granier & Deloffre, 1993, non 1968; topotypic material (Collection Deloffre, Leg. Radoičić) ; **a** Oblique section; **b** Oblique section; **c** Longitudinal section ; **d** Fragment in a transverse section. Scale bar = 0.5 mm.

It is suggested that the fertile part of these algae is decreasing gradually from the ancestral endosporate and cladosporate forms to the choristoporate form with specialized ampulae. As in genuine cladosporate forms (such as *Triploporella steinmanni*) the fertile part is mostly concentrated in the primary laterals, we would expect similar ratio for most cladosporate species. With primary laterals representing only 12.9% of the total volume of the cytoplasm, *Harlanjohnsonella annulata* does not fit with this model. Hypothesis 2 should therefore be favoured; as a result, *Harlanjohnsonella annulata* is probably an endosporate species.

CONCLUSION

The Cenomanian *Harlanjohnsonella annulata* Elliott in Granier & Deloffre, 1993, is reported for the first time outside its type area, *i.e.*, in Lebanon, and in older strata, *i.e.*, Late Barremian or Bedoulian in age. In these specimens, as well as in topotypic material of *Harlanjohnsonella annulata* that we examined (Collection Deloffre, Leg. Radoičić), we did not observed any evidence of secondary laterals. On the basis of an investigation on the distribution of the cytoplasmic volume, it is suggested that the reproductive strategy of *Harlanjohnsonella annulata* was most likely endosporate, not cladosporate.

ACKNOWLEDGEMENTS

We would like to thank the CNRSL (National Council for Scientific Research-Lebanon) and the AUF (University Agency of the Francophony) for their financial support. This research is a contribution to the project N° 30959NJ - PHC CEDRE 2014; supported by of the research project of Hubert-Curien Partnership program (PHC) CEDRE, implemented in Lebanon and France by the Ministry of Foreign Affairs (Ministère des Affaires étrangères, MAE) and the Ministry of Higher Education and Research (Ministère de l'Enseignement Supérieur et de la Recherche, MESR). This paper is a contribution of the team project "Biodiversity: Origin, Structure, Evolution and Geology" led by Dany Azar at the Lebanese University. The thin sections are deposited with LPB numbers in the collections the Département des Sciences de la Terre et de l'Univers, Université de Bretagne Occidentale, Brest (France). Finally, we would like to thank Filippo Barattolo, Ioan I. Bucur and Mariano Parente for their constructive comments.

REFERENCES

Barattolo, F., 1983. Observazioni su *Triploporella steinmannii* n. sp. (alghe Verdi, Dasicladali) del Cretacico del Messico. Bollettino della Società dei Naturalisti in Napoli, 91 (1982): 1–53.

Bassoullet, J.-P., Bernier, P., Conrad, M.A., Deloffre R. & Jaffrezo, M., 1978. Les algues Dasycladales du Jurassique et du Cretacé. Géobios, Mémoire spécial 2, 330 pp.

Berger, S., 2006. Photo-Atlas of living Dasycladales. Carnets de Géologie [Notebooks on Geology], CG2006_B02, 348 pp.

Bucur, I.I., 2007. *Salpingoporella*? *popgrigorei*, a new species of Dasycladales (calcareous algae) from the Lower Aptian deposits of Pădurea Craiului (northern Apuseni Mountains, Romania. Facies, 53: 377-388.

Elliott, G., 1968. Three new Tethyan Dasycladaceae (calcareous algae). Paleontology, 11(4): 491-497.

Granier, B. & Deloffre, R., 1993. Inventaire critique des algues dasycladales fossiles II. Partie - les algues dasycladales du Jurassique et du Crétacé. Revue de Paléobiologie, 12 (1): 19-65.

Granier, B., Lethiers, A. & Sander, N.J., 2013. The XXIst Century Edition of the "New studies on Triassic Siphoneae verticillatae, by Julius von Pia. Jahrbuch der Geologischen Bundesanstalt, 153(1-4): 239-300.

Granier, B. & Sander, N.J., 2013. The XXIst Century (the 100th Anniversary) Edition of the "New studies on Triassic Siphoneae verticillatae" by Julius von Pia. Carnets de Géologie [Notebooks on Geology], CG2013_B01, 108 pp. [56 videos].

Jaffrezo, M., Poisson, A. & Akbulut, A., 1980. Les Algues du Crétacé Inférieur des séries de type Bey Daglari (Taurides Occidentales, Turquie. Bulletin of Mineral Research and Exploration Institute of Turkey, 91: 76-88.

Maksoud, S., Granier, B., Azar, D., Gèze, R., Paicheler, J.-C., Clavel, B. & Moreno-Bedmar, J.A., 2014, in press. Revision of "Falaise de Blanche" (Lower Cretaceous) in Lebanon, with the definition of a Jezzinian Regional Stage, and its micro-paleontological characterization. Carnets de Géologie [Notebooks on Geology], 14(18).

Pia, J. von, 1912. Neue Studien über die triadischen Siphoneae verticillatae. Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, 25: 25-81.

Pia, J. von, 1920. Die Siphoneae verticillatae vom Karbon bis zur Kreide. Abh. zool.-bot. Gesellschaft, 11 (2): 263 pp. [Les Siphonées verticillées du Carbonifère au Crétacé. Éditions Technip, 1961].

Radoičić, R., 1995. Contribution to the study of Cretaceous biostratigraphy of Zlatibor Mountain. Radovi Geoinstituta, 31: 17–30 [in Serbo-Croatian with English abstract].

Radoičić, R. & Schlagintweit, F., 2010. Observations on *Dissocladella annulata* (Elliott, 1993) nov. comb. (Calcareous algae, Dasycladales) from the Cenomanian of west Serbia. Annales Géologiques de la Péninsule Balkanique, 71: 53-71.

TABLES

Table 1 Averages and Standard Deviations of the measured parameters of the *Harlanjohnsonella annulata* specimens found in Lebanon. The units for D, d, e, h, l, and p are given in mm; d/D in %. L: maximum length; D: external diameter; d: central stem diameter; h: interverticillar distance of two successive whorls = from a reference plane in one whorl to the same plane in the next; l: length of the laterals; p: width of primary laterals; e: thickness of the calcareous wall; w: number of laterals per verticil.

Specimen	D	d	d/D	e	h	l	p	w
VO15-12					0.162	0.213	0.106	36
VO11-3	1.702	1.425	83.73	0.139	0.184	0.148	0.127	36
VO15-44	1.734	1.617	93.25	0.059		0.117	0.117	36
VO41-4	1.814	1.592	87.76	0.111	0.179	0.148	0.111	
VO14-23	1.463	1.073	73.34	0.195		0.219	0.122	40
VO59-10	1.915	1.414	73.84	0.251		0.243	0.122	60
VO19-21	1.707	1.414	82.84	0.147		0.122	0.121	40
VO16-26					0.171	0.195	0.122	
VO11-27					0.146	0.171	0.122	
VO18-05	1.951	1.707	87.49	0.122		0.122	0.098	40
VO38-10	2.341	1.854	79.20	0.244		0.244	0.122	52
Average (µ)	1.828	1.512	82.681	0.158	0.168	0.177	0.117	42.50
Standard deviation (σ)	0.256	0.237	6.963	0.067	0.015	0.049	0.009	8.80

Table 2 Averages and Standard Deviations of the measured parameters from a topotypic material (Collection Deloffre, Leg. Radoičić). The units for D, d, e, h, l, and p are given in mm; d/D in %.

Specimen	D	d	d/D	e	h	l	p	w
a	1.268	0.976	76.97	0.146	0.244	0.122	0.122	
b	1.024	0.880	85.94	0.072	0.195	0.097	0.073	
c	1.585	1.341	84.61	0.122	0.231	0.122	0.122	25
d	1.610	1.366	84.84	0.122		0.146	0.122	30
e	1.366	1.171	85.72	0.098	0.210	0.098	0.122	27
f	1.226	0.980	79.93	0.123	0.170	0.122	0.098	
g	1.220	0.927	75.98	0.147		0.122	0.098	27
h	1.317	1.024	77.75	0.147		0.121	0.098	40
i	1.220	0.902	73.93	0.159	0.170	0.146	0.073	
j	1.710	1.341	78.42	0.185	0.170	0.146	0.122	
k	1.707	1.268	74.28	0.220		0.146	0.098	45
l	1.317	1.073	81.47	0.122		0.122	0.098	27
m	1.366	1.122	82.14	0.122				28
Average (µ)	1.380	1.105	80.15	0.137	0.199	0.126	0.104	31.13
Standard deviation (σ)	0.211	0.177	4.30	0.037	0.031	0.017	0.018	7.28

Table 3 Summary of the biometric data of *Harlanjohnsonella annulata*. *Sample VO 41 (thin section VO 41-0). The units for D, d, e, h, l, and p are given in mm; d/D in %.

Measurements	*Harlanjohnsonella annulata*			
	Elliott, 1968	Radoičić & Schlagintweit, 2010	This work (μ ± σ)	
			Topotype material (Collection Deloffre)	Our material
L	> 6	12		≈ 5 *
D	2	1.18–3.10	1.380 ± 0.211 (13)	1.828 ± 0.256 (8)
d	-	0.940–2.590	1.105 ± 0.177 (13)	1.512 ± 0.256 (8)
d/D	0.74	71–89.5	80.15 ± % 4.30 (13)	82.68 ± 6.963 (8)
e	0.26	0.098–0.247	0.137 ± 0.037 (13)	0.158± 0.067 (8)
h	0.19-0.25	0.198–0.210	0.199 ± 0.031 (7)	0.168 ± 0.015 (5)
l	-	-	0.126 ± 0.017 (12)	0.177 ± 0.049 (11)
p	-	0.098–0.123	0.104 ± 0.018 (12)	0.117 ± 0.009 (11)
w	48-50	35–70	~30.5 ± 8.05 (8)	42.5 ± 8.80 (8)
w’’	0	5 to 6	0	0

Table 4 Comparison table (minimum – maximum values) of *Harlanjohnsonella annulata*. The units for D, d, h, l, and p are given in mm.

	Radoičić & Schlagintweit, 2010	Our material	Topotype material (Collection Deloffre)
Parameter	Minimum - Maximum values		
D	1.180 - 3.100	1.463 - 2.341	1.710 - 1.024
d	0.940 - 2590	1.073 - 1.854	0.880 - 1.341
h	0.198 - 0.210	0.146 - 0.184	0.170 - 0.244
l	0.098 - 0.247	0.117 - 0.244	0.097 - 0.146
p	0.098 - 0.123	0.098 - 0.127	0.073 - 0.122
w	35 - 70	36 - 60	25 - 45

Table 5 Biometric data of *Harlanjohnsonella* cf. *annulata* as measrued on the original thin-section (Collection Jaffrezo, thin section 881 E10). The units for D, d, e, h, l, and p are given in mm.

D	d	d/D	e	h	l	p
1.471	1.176	79.94%	0.147	0.088	0.159	0.147

Table 6 Biometric data of *Triploporella steinmanni* (from Barattolo, 1983). The units for D, d, h, l, l2, p1, p1', and p2 are given in mm; d/D in %.

	D	d	d/D	h	l	p1= p'v	p1'=p'w	l2=l''	p2=p''	w	w'
minimum	3.2	0.9	28.13	0.32	1	0.28	0.28	0.16	0.13	26	-
maximum	4.2	1.5	35.71	0.4	1.3	0.37	0.41	0.23	0.16	34	-
Average (µ)	3.96	1.21	30.56	-	-	0.33	-	-	-	30.7	3
Standard deviation (σ)	0.25	0.23				0.04				3.4	

Table 7 Averages and Standard Deviations of the measured parameters of *Montiella elitzae* from our material. The units for D, d, h, ls, ps, lf, pf are given in mm; d/D in %.

	D	d	h	ls	ps	lf	pf	w
MEB45-34	0.707	0.159	0.164	0.195	0.049	0.195	0.146	
MEB45-37	0.768	0.268	0.175	0.122	0.073	0.244	0.171	8
MEB45-25	0.610	0.171				0.195	0.146	7
MEB45-12	0.756	0.220	0.148	0.268	0.073	0.220	0.171	6
MEB45-10	0.730	0.171		0.244	0.049	0.220	0.146	6
MEB45-11	0.585	0.171	0.158	0.220	0.049	0.195	0.149	6
MEB19-52	0.745	0.213	0.276	0.213	0.042	0.213	0.149	
MEB49-14	0.609	0.146		0.243	0.097	0.170	0.121	6
MEB38-32	0.731	0.146		0.292	0.097	0.243	0.170	6
MEB49-02	0.731	0.195		0.219	0.048	0.146	0.121	8
Average (µ)	0.697	0.186	0.184	0.224	0.064	0.204	0.149	7
Standard deviation (σ)	0.068	0.038	0.052	0.048	0.022	0.031	0.018	1

Table 8 Measurements of *Dasycladus vermicularis* in millimeter (from Berger, 2006).

d	h	w	ls1	ps1	ls2	ps2	w'	ls3	ps3	w''	lf	d
0.45	0.53	10	0.85	0.15	0.50	0.05	4	0.25	0.025	4	0.30	0.45

Table 9 Measurements of *Neomeris dumetosa* in millimeter (from Berger, 2006).

d	h	w	ls1	ps1	ls2	ps2	w'	ls2'	ps2'	lf	pf
0.29	0.07	28	0.36	0.04	0.22	0.03	2	0.11	0.09	0.12	0.09

Table 10 Volume ratio of *Harlanjohnsonella annulata, Montiella elitzae* and *Triploporella steinmannii*. In this table we assume as a starting hypothesis that the laterals of *Harlanjohnsonella* are fertile and its main axis sterile. The units for D, d, h, ls, ps, lf, pf, p'f are given in mm; VO, vs, Vs, vf, Vf in mm^3; d/D in %.

Parameter	*Harlanjohnsonella* hypothesis (1)	*Harlanjohnsonella* hypothesis (2)	*Triploporella*	*Montiella*
D	1.828	1.828	3.96	0.697
d	1.512	1.512	1.21	0.186
h	0.168	0.168	0.40	0.184
ls	-	0.177	0.23	0.224
ps	-	0.117	0.16	0.064
lf	0.177	-	1.30	0.204
pf	0.117	-	0.33	0.149
p'f	-	-	0.41	-
w	42.5	42.5	31.0	8.0
w'	-	-	3.0	-
Calculated volumes				
V0 (stem)	0.302	0.302	0.460	0.005
vs (1 sterile lateral)	-	0.001	0.005	0.001
Vs (total laterals)	-	0.045	0.142	0.006
VS (total sterile part) = V0 + Vs	0.302	0.045	0.602	0.011
vf (1 fertile lateral)	0.001	-	0.138	0.002
VF (total fertile)	0.045	0.302	4.241	0.019
Ratios				
R0 (V0/Vtotal)	87.06	87.06	9.50	16.81
RS (VS/Vtotal)	87.06	12.94	12.43	36.24
RF(VF/Vtotal)	12.94	87.06	87.57	63.76
R-laterals (F/F+S)	100.00	0.00	90.87	76.64
Cysts	cladosporate	endosporate	cladosporate	choristosporate

Table 11 Absolute and Relative Volumes of *Dasycladus vermicularis*.

Volumes	V0	0.0835
	vs1	0.0150
	vs2	0.0010
	vs3	0.0001
	vs (of one sterile lateral) = vs1+[w'* (vs2+(w''*vs3)]	0.0209
	VS = V0 + w*vs	0.2926
	vf	0.0141
	VF = w*vf	0.1414
Ratios	R0 (V0/Vtotal)	19.24%
	RS (VS/Vtotal)	67.42%
	RF(VF/Vtotal)	32.58%
	R-laterals (F/F+S)	40.34%
	Cysts	choristosporate

Table 12 Absolute and Relative Volumes of *Neomeris dumetosa.*

Volumes	V0	0.0046
	vs1	0.0006
	vs2 (cylinder part)	0.0001
	vs2' (sphere part)	0.0004
	vs (of one sterile lateral) = vs1+ w'*(vs2+vs'2)]	0.0017
	VS = V0 + w*vs	0.0511
	vf	0.0005
	VF = w*vf	0.0153
Ratios	R0 (V0/Vtotal)	6.90%
	RS (VS/Vtotal)	76.88%
	RF(VF/Vtotal)	23.12%
	R-laterals (F/F+S)	24.83%
	Cysts	choristosporate

Table 13 Comparisons of the relative volumes. R0, ratio of the stem to the total volume; R fertile laterals, ratio of the fertile laterals to the total volume; R sterile laterals, ratio of the sterile laterals to the total volume; R laterals (F/F+S), ratio of the fertile laterals to the laterals, fertile and sterile; R laterals (fertile + sterile), ratio of the laterals, both fertile and sterile, to the total volume; RS (TOTAL), ratio of the sterile parts to the total volume; RF (TOTAL), ratio of the fertile parts to the total volume.

Species	*H. annulata*	*T. steinmannii*	*M. elitzae*	*D. vermicularis*	*N. dumetosa*
Family	Triploporellaceae	Triploporellaceae	Dasycladaceae	Dasycladaceae	Dasycladaceae
Tribe	Salpingoporelleae	Triploporelleae	Neomereae	Dasycladeae	Neomereae
d	1.512 (average)	1.210 (average)	0.186 (average)	0.450	0.286
Ratios					
R0 (stem)	87.06	9.50	16.81	19.24	6.90
R fertile laterals	12.94 (1) or 0.00 (2)	87.57	63.76	32.58	23.12
R sterile laterals	0.00 (1) or 12.94 (2)	2.93	19.43	48.18	69.99
R laterals (F/F+S)	-	90.87	76.64	40.34	24.83
R laterals (fertile + sterile)	12.94	90.50	83.19	80.76	93.10
RS (TOTAL)	87,06 (1) ou 12,94 (2)	12.43	36.24	67.42	76.88
RF (TOTAL)	12,94 (1) ou 87,06 (2)	87.57	63.76	32.58	23.12
Cysts	clado- (1) or endo- (2) sporate	cladosporate	choristosporate	choristosporate	choristosporate